TAXONOMY OF THE WATER ASHES: FRAXINUS CAROLINIANA, F. CUBENSIS, AND F. PAUCIFLORA (OLEACEAE)

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ABSTRACT

Water ash has commonly been identified as a single species, Fraxinus caroliniana Miller, but is here recognized to comprise three distinct entities each treated at specific rank: (1) F. caroliniana sensu stricto, from northern Florida west along the Gulf Coast to Texas and Oklahoma and north along the Atlatic coast to Virginia; (2) F. cubensis Griseb., from Cuba and the southern two-thirds of the Florida peninsula; and (3) F. pauciflora Nutt., from northern Florida and southern Georgia. All three are similar in gross morphology and occur in swampy or riverine habitats but the ranges of F. caroliniana and F. cubensis are essentially parapatric, while the range of F. pauciflora lies mostly within that of F. caroliniana and overlaps with F. cubensis. Samaras of F. caroliniana sensu stricto are broad, often rhombic-elliptic, (11–)13–19-nerved per side, and 3-winged at a low frequency, while those of F. cubensis are narrower, 5–9-nerved per side, and consistently 2-winged. Samaras of F. pauciflora are similar in shape to those of F. cubensis, but the abaxial leaf surfaces are covered by a cuticular micro-reticulum similar to that characteristic of the F. americana complex. County-level distributions are mapped and a key, descriptions, and typifications are provided. A lectotype is designated for Fraxinus hybrida Lingelsheim.

KEY WORDS: Fraxinus caroliniana, Fraxinus cubensis, Fraxinus pauciflora, Florida

The name Fraxinus caroliniana Miller is currently commonly used in southeastern USA herbaria and floristic accounts to identify various expressions of water ash — all with samara bodies flat and winged nearly to the base. This broad view has been adopted by Miller (1955), Long and Lakela (1976), Duncan and Duncan (1988), Godfrey (1988), Wallander (2008), and Weakley (2010) and by Wunderlin and Hansen (2003, 2010) even to include another swamp species, F. profunda (Bush) Bush, in synonymy. Brown and Kirkman (1990) and Nelson (1995) separated F. profunda but identified all water ash as F. caroliniana without citing synonyms. Long and Lakela (1976, p 687) were particularly emphatic: "This species [F. caroliniana] is extremely variable, but variations scarcely deserve taxonomic recognition." Other students of the woody flora of northern and central Florida, however, have maintained F. profunda as a separate species and recognized a distinction between F. caroliniana and F. pauciflora Nutt. (e.g., Sargent 1894, 1902; Small 1913; Kurz & Godfrey 1962; Clewell 1985; Nesom 2010), using characters similar to those in the present study. Fraxinus cubensis Griseb. of southern Florida apparently has never been recognized in the USA, but it has been treated as F. caroliniana var. cubensis (Griseb.) Lingelsh. in the Cuban flora (Leon & Alain 1957).

In working out a taxonomic treatment of Fraxinus for the developing FNANM volumes, it became evident that "water ash" includes three entities. In addition to the trees with characteristically broadly elliptic to rhombic and often 3-winged samaras (= F. caroliniana sensu stricto), others produce narrower, consistently 2-winged and differently veined samaras. Then, after becoming familiar with the distinctive abaxial leaf surface of F. americana L. (white ash), I saw that some trees with the more narrowly 2-winged samaras have an abaxial foliar morphology similar to F. americana and stand apart from the other water ashes. Field observations confirm the distinctiveness of these (identified as F. pauciflora, termed here as "swamp white ash"). In overview, each of the three

expressions of water ash is recognized here at specific rank: F. caroliniana, F. pauciflora, and F. cubensis.

Trees of these three taxa are generally similar in vegetative features and all grow in swampy or riverine habitats, often or characteristically with their bases submerged. The key below separates them on the basis of features of the samaras and abaxial foliar epidermis. Fraxinus profunda is added to the key since it has sometimes been confused with water ash in Florida. All are contrasted with F. americana, a species of upland woods with a different samara morphology.

- 1. Samara bodies plump-subterete, wings 3–7 mm across at widest point, lateral veins 3–5 on each side of the wing, all originating from near the top of the body, essentially parallel with the wing margins; upland habitats Fraxinus americana 1. Samara bodies flattened, wings 8–22 mm across at widest point, lateral veins 5–9 or 11–19 on each side of the wing, originating in sequence from along the major vein paralleling the body edge, angling upward; swamp and riverine habitats.
 - 2. Large trees; leaflets (7-)9-15(-25) cm x (2.5-)3.5-7(-11) cm, bases often rounded, less commonly obtuse to acute or acuminate; samaras (35-)40-70(-75) mm, wings gradually expanded from near the base of the body to proximal 1/2, (5.5-)6-10(-12) mm wide Fraxinus profunda 2. Shrubs to small trees; leaflets mostly (4-)5-11(-12) cm x (1.5-)2-5(-6) cm, bases obtuse to acute or abruptly attenuate; samaras (25–)30–50 mm, wings expanded gradually from near base, (10-)12-20(-22) mm or 6-10(-12) mm wide.
 - 3. Leaflet abaxial surfaces micro-foveolate-papillose (use 20–40X lens) with a cuticular reticulum overlaying and obscuring the epidermal surface, minute glandular peltate scales not evident Fraxinus pauciflora 3. Leaflet abaxial surface without a cuticular overlay, the epidermal surface visible, minute glandular peltate scales usually evident and abundant.
 - 4. Samaras $35-46 \times (10-)12-20(-22)$ mm, rhombic to broadly elliptic, elliptic-obovate, oblong-obovate, or rhombic-ovate, wings 2-3, lateral veins (11-)13-19 on each side of the wing; fruit body usually half or more than half the length of the samara
 - Fraxinus caroliniana 4. Samaras $(25-)30-50(-54) \times 6-10(-12)$ mm, obovate-oblanceolate to narrowly obovate or narrowly elliptic-obovate, wings 2, lateral veins 5–9 on each side of the wing; fruit body half or less than half the length of the samara Fraxinus cubensis
- FRAXINUS CAROLINIANA Miller, Gard. Dict., ed. 8. 1768. Calycomelia caroliniana (Miller) Kostel., Allg. Med.-Pharm. Fl. 3: 1004. 1834. Leptalix caroliniana (Miller) Raf., Alsographia Amer. 36. 1838. Fraxinus americana var. caroliniana (Miller) D.J. Browne, Trees America 398. 1857. Fraxinus nigra subsp. caroliniana (Miller) Wesmael, Bull. Soc. Roy. Bot. Belgique 31: 113. 1892. TYPE: USA. "Raised from seeds which were sent from Carolina in the year 1724, by Mr. Catesby" (K).
- Fraxinus platicarpa Michx., Fl. Bor.-Amer. 2: 256. 1803. Calycomelia platicarpa (Michx.) Kostel., Ind. Hort. Bot. Prag. 26. 1844. Fraxinus caroliniana var. platicarpa (Michx.) Lingelsh., Bot. Jahrb. Syst. 40: 221. 1908. TYPE: USA. "HAB. in Carolina" (P presumably).
- Fraxinus pallida Bosc, Mém. Cl. Sci. Math. Inst. Natl. France 1808: 201. 1809. Leptalix pallida (Bosc) Raf., Alsogr. Amer. 33. 1838. Calycomelia pallida (Bosc) Kostel., Ind. Hort. Bot. Prag. 26. 1844. As synonym of F. caroliniana fide Sargent (1894).

- Fraxinus caroliniana Miller var. latifolia Roemer & Schultes, Syst. Veg. 1: 279. 1817. TYPE: USA. Protologue: "A Pensylvania ad Carolinam, rarius." As synonym of F. caroliniana based on geography.
- Fraxinus triptera Nutt., Gen. N. Amer. Pl. 2: 232. 1818. Samarpses triptera (Nutt.) Raf., New Fl. 3: 93. 1838 ("1836"). Fraxinus platicarpa Michx. var. triptera (Nutt.) A.W. Wood, Class-Book Bot., ed. 1861. 598. 1861. Fraxinus americana var. triptera (Nutt.) D.J. Browne, Trees America 399. 1857. TYPE: USA. South Carolina. (Holotype: PH?). Protologue: "8. triptera. Leaflets (about 7?) obovate, entire, subsessile, beneath tomentose, oblique at the base; samara very broad, elliptic-obovate, most 3-winged! attenuated at the base. HAB. In the oak-forests of South Carolina. Fruit at first sight almost similar to Halesia, more rarely 2 than 3 winged, the seed also 3-sided. Points of the leaves obtuse, the under side paler and softly villous, the common petiole and nerves beneath smooth." Treated by Nuttall as a different species than his "5. caroliniana" and "6. platycarpa."

Nuttall later added comments (1849, p. 63): "I observed fruit of this curious species many years ago, in winter, in the oak forests of South Carolina, and as I thought, the leaves of the same; but I am now in doubt whether the leaves than collected actually belonged to the same plant with the fruit. I must therefore leave the species in the same imperfect manner I than found it, as I have never since seen any other specimen. [paragraph] The fruit is the most curious of any in the genus, at first sight almost similar to that of an Halesia, being nearly of the same breadth; the samara, in fact, appeared to be more rarely 2 than 3 winged, the seed itself was also 3-sided, at the base the fruit is attenuated into a very slender peduncles without being at all terete. Perhaps it is merely a variety of F. platycarpa."

- Fraxinus curvidens Hoffsgg., Verz. Pfl.-Kult., Nachtr. 2: 29, 118. 1826. As a synonym of F. caroliniana fide Sargent (1894).
- Fraxinus cordata Raf., Alsographia Amer. 34. 1838. TYPE: Florida. "139. Fr. L. [Leptalix] cordata Raf. foliolis petiol. ovatis ellipt. integris, basi subcordatis, apice attenuatis obtusis. supra reticul. glabris lucidis, subtus glaucis pubescens—very distinct sp. from Florida, disc. by Kin, large folioles 4 to 6 inches long 2 or 3 broad." As synonym of F. caroliniana fide Wunderlin and Hansen (2010), but Rafinesque's description of the leaflet bases as "subcordate," emphasized by the epithet, does not correspond to known native ashes of Florida.
- Fraxinus platicarpa Michx. var. oblanceolata M.A. Curtis, Amer. J. Sci. Arts 57: 408. 1849. Fraxinus caroliniana var. oblanceolata (M.A. Curtis) Fernald & Schub., Rhodora 50: 188. 1948. TYPE: USA. South Carolina. Berkeley Co.: Santee Canal, Santee swamp, [no date], H.W. Ravenel s.n. (holotype: CHARL?; isotypes: GH, NY!).
- Fraxinus platicarpa Michx. var. pubescens M.A. Curtis, Amer. J. Sci. Arts 57: 408. 1849. Fraxinus caroliniana var. pubescens (M.A. Curtis) Fernald, Rhodora 39: 442. 1937. Fraxinus caroliniana forma pubescens (M. A. Curtis) Fernald & Schubert, Rhodora 50: 188. 1948. TYPE: USA. South Carolina. Berkeley Co.: Santee Canal, Santee swamp, [no date], H.W. Ravenel s.n. (holotype: CHARL?; isotypes: GH, NY!).
- Fraxinus nuttallii Buckley, Proc. Acad. Nat. Sci. Philadelphia 12: 444. 1860. TYPE: USA. Alabama. Wilcox Co.: In swamps, no date, Buckley s.n. (PH?). For this small swamp tree with 3winged fruits, Buckley noted that "As Nuttall had not material for a complete description, none can tell what is meant by his Fraxinus triptera; but as possibly he may have intended the tree now described, I call it Nuttall's Ash." As synonym of F. caroliniana based on morphological description and geography.
- Fraxinus rehderiana Lingelsh. in Engler, Pflanzenr. 4(Heft 72): 42. 1920. Fraxinus caroliniana var. rehderiana (Lingelsh.) Sargent, J. Arnold Arbor. 2: 173. 1921. TYPE: USA. Virginia. Isle of Wight Co.: Banks of Blackwater River near Zuni, 19 Aug 1908, A. Rehder s.n. (holotype: B?; isotype: GH). Lingelsheim made this observation: "Species fortasse hybrida, e F. pennsylvanica et F. caroliniana orta, forma parallela F. hybridae." Placed here as a synonym

of F. caroliniana based on its morphological description and geography and on Sargent's assessment.

Fraxinus caroliniana Miller forma hypomalaca Fernald & Schubert, Rhodora 50: 189. 1948. TYPE: USA. Virginia. Greensville Co.: Fontaine Creek, SW of Haley's Bridge, cypress swamp, wooded bottomland, 9 Jul 1946, M.L. Fernald & H.E. Moore 15139 (holotype: GH!; isotype: GH!, PH).

Fraxinus caroliniana Miller forma lasiophylla Fernald & Schubert, Rhodora 50: 189. 1948. TYPE: USA. Virginia. Southampton Co.: Darden's Pond N of Courtland, upper border of sandy and peaty shore, 15 Sep 1946, M.L. Fernald, B.H. Long, and I.D. Clement 15335 (holotype: GH!; isotype: GH!, PH).

Trees or shrub-like trees with several leaning trunks and often with buttressed bases, 2.5–10(-15) m; twigs terete; bark light gray, with thin appressed scales, not deeply furrowed; winter buds brown. Leaves deciduous, pinnate, 12–40 cm, leaflets 5–7(–9), glabrous on both surfaces or sparsely pubescent abaxially along the veins, rarely over the surface, dark green adaxially, paler or whitish abaxially, not scaly-punctate, not papillose, blades 4–12(–15) cm x (1–)2–3(–6) cm, lanceolate to ovate-lanceolate, elliptic, or elliptic-oblong, lateral vein pairs (5–)7–9(–12), apex obtuse to acute or acuminate, base obtuse to truncate or rounded, margins shallowly serrate to crenulate on distal 4/5–2/3, lateral petiolules 2–3(–15) mm, not winged; rachis (2–)3–9(–12) cm; petiole bases not raised; leaf scars shallowly hemispheric to depressed obovate, apex very slightly convex or notched. Flowers unisexual (species dioecious), appearing before leaves, wind-pollinated; pistillate calyx present, persisting or not; petals absent. Samaras 35–46 mm, rhombic to broadly elliptic, elliptic-obovate, oblong-obovate, or rhombic-ovate, body flattened and abruptly acuminate to stipitate at the base, usually half or more than half the length of the samara, wings 2(–3), arising from the base or proximal 1/4 of body, (10–)12–20(–22) mm wide; lateral veins (11–)13–19 on each side of the wing.

Flowering Feb-Apr(-May). River and stream banks, alluvial woods, flatwoods, cypress-gum swamps (often in water), overcup oak-water locust-water elm, swamp and pond margins, depressions, ditches and canals, roadside swales; 3–60(–100) m; Ala., Ark., Fla., Ga., La., Miss., N.C., S.C., Tex., Va. Water ash, pop ash.

FRAXINUS CUBENSIS Griseb., Cat. Pl. Cub. 170. 1866. Fraxinus caroliniana var. cubensis (Griseb.) Lingelsh., Bot. Jahrb. Syst. 40: 221. 1908. Fraxinus caroliniana subsp. cubensis (Griseb.) Borh., Bot. Közlem 58: 176. 1971. Fraxinus pennsylvanica subsp. cubensis (Griseb.) E. Murray, Kalmia 13: 6. 1983. Fraxinus pennsylvanica var. cubensis (Griseb.) E. Murray, Kalmia 13: 6. 1983. TYPE: Cuba. Protologue: "Cuba occ., in depressis pr. Zarabanda," 1865, C. Wright 45 (holotype: GOET; isotype: K digital image!)." Collections at GH and NY (2 sheets) are possible type material — Cuba, without other collection data, C. Wright 3624 — if, as in Wright collections from the southwestern USA, field numbers and published collection numbers are inconsistent. The GOET and K labels, however, specify "Wright 45." Another possible type specimen (S digital image!) has a Charles Wright label but is unnumbered.

Small trees or shrubs 3–14 m, sometimes multi-trunked from the base; twigs terete; bark grayish to gray-brown, morphology; winter buds reddish brown to brown. Leaves deciduous, pinnate, 12–23 cm, spaced along branches; leaflets (3–)5(–7), subcoriaceous, glabrous on both surfaces except hirsute-pilose along abaxial midvein and lateral vein axils, rarely puberulent-hirsute on abaxial lamina, green to yellowish green, scaly-punctate abaxially, not papillose, blades (4–)4.5–10.5(–13) cm x (1.5–)2–5(–5.5) cm, narrowly to broadly elliptic to elliptic-obovate or obovate, apex acute to acute-acuminate, lateral vein pairs 7–11, base acute to obtuse, margins shallowly serrate to denticulate on distal 1/2–2/3, lateral petiolules 4–10 mm, not winged; rachis 4.5–10 cm, not winged; petiole bases not raised; leaf scars transversely elliptic and shallow concave, 3–5 mm wide. Flowers

unisexual (species dioecious), appearing before the leaves, wind pollinated; pistillate calyx present and persisting at base of samaras; petals absent. Samaras (25-)30-50(-54) mm, obovateoblanceolate to narrowly obovate or narrowly elliptic-obovate, body flattened, half or less than half the length of the samara, wings 2 (very rarely 3), arising from middle/proximal 3/4 of body, 6–10(– 12) mm wide, lateral veins 5–9 on each side of the wing.

Flowering Feb-Mar. Hardwood hammocks, swamp forests and low woods, apparently most commonly along river and creek banks and pond and lake edges; 0–5 m; Fla.; West Indies (Cuba). Cuban water ash

I have seen collections of Fraxinus cubensis from the following Florida counties: Brevard, Citrus, Collier, Glades, Highlands, Hillsborough, Lee, Manatee, Marion, Martin, Monroe, Okeechobee, Orange, Palm Beach, Polk, Sarasota, and Sumter. Various localities on the shores of Lake Okeechobee are in Glades, Martin, Okeechobee, and Palm Beach counties.

Specimens examined from CUBA: Prov. Santa Clara, Peninsula de Zapata, on the edge of Ciénaga de Zapata, in swampy forests, small tree, 1 Feb 1924, Ekman 18368 (NY); Prov. Matanzas, Mpio. Martí, Ciénaga del Majaguillar al NO de Martí, Ciénaga de Gonzalito cerca del Canal de Blanquizal, 5 m, bosque secundario de ciénaga, 20 Feb 2009, Greuter 27019 (NY); Cayo la Lisa, Ciénaga de Zapata, Las Villas 24 Feb 1941, León et al. 19562 (NY); Los Sabados, Hacienda El Jiqui, Peninsula de Zapata, 16 Jul 1920, Roig & Gemata 2145 (NY); Prov. Matanzas: Ciénaga de Zapata, along road between Australia and Playa Larga, close to Calal de La Laguna, evergreen or semievergreen forest on limestone, temporarily inundated, 13 Apr 1995, Rova et al. 2261 (GOET digital image!, DNA voucher). All are localities in western Cuba, just east of Havana.

Fraxinus cubensis is similar to F. caroliniana in most features except fruit morphology (I have not seen F. cubensis in nature, however, to provide a comparison of its growth habit). Samaras of Fraxinus caroliniana appear to be far more variable than those of F. cubensis (Figs. 4 and 5), and although narrower samaras of F. caroliniana may approach of those of F. cubensis in outline, the distinction in venation is consistent (as in the key above). It might seem justifiable to treat the two as conspecific, but the remarkably sharp divide in geographical distribution would appear to mark some kind of biological isolation and I have not observed unequivocal intermediates in samara morphology. It will be interesting to investigate the area of apparent parapatry toward evaluation of their apparent reproductive isolation, as hypothesized here.

Samaras of Fraxinus caroliniana are 3-winged (3-carpellate) at a low frequency (ca. 5–20%) on an individual) over the whole range of the species and it is more common than not to find 3winged fruits on any single specimen. Samaras of F. cubensis are consistently 2-winged, but I have encountered 2 collections with 3-winged fruits: Manatee Co., Palmetto, 21-23 Aug 1895, Nash 2431 (GH); Sumter Co., Sumter Citrus Wildlife Management Area, W of Bushnell, Withlacoochee River bottoms, 13 Aug 1958, Kral 7847 (GH).

FRAXINUS PAUCIFLORA Nutt., N. Amer. Sylva 3: 61, plate 100. 1849. TYPE: USA. Georgia. [Charlton Co.:] "collected in Georgia in the neighborhood of 'Trader's Hill,' by the late indefatigable and excellent botanist, Dr. Baldwyn," no date (holotype: PH; possible isotype: PH).

Fraxinus platicarpa Michx. var. floridana Wenzig, Bot. Jahrb. Syst. 4: 185, plate II, 11. 1883. Fraxinus floridana (Wenzig) Sargent, N. Amer. Silva 14: 39. 1902. TYPE: USA. Florida: "Cabanis! in hb. Berol." (holotype: B?, fragment GH). "Samara calycis dentibus parvis triangularibus saepe destructis, lanceolata, alae margo in longitudinem lateris partis inferioris latior quam in Fr. quadrangulata Mchx., angustior quam in Fr. platycarpa, apice obtusissima emarginata basi acuminato-attenuata. 0,054 m. longa, ala 0,040 m. lata, pars inferior 0,027 m long, plana, longitudinaliter sulcata." A GH collection from 1830 by E.F. Leitner is noted to be a possible type, but the protologue indicates that the type was collected by Jean Louis Cabanis (1816–1906) — see bibliographic notes by Sargent (1902, p. 39).

Fraxinus hybrida Lingelsh., Bot. Jahrb. Syst. 40: 220. 1908. LECTOTYPE (designated here): USA. Florida. Duval Co.: swamps, near Jacksonville, Aug [1890?], Curtiss 2321 (NY!; isolectotypes: GH-2 sheets!). Lingelsheim cited as syntypes "Curtiss 2321!, Nash 941!, 1698!"—Nash 941 (E digital image!) and Nash 1698 (E digital image!, GH!). Curtiss made a series of collections of this species in July and August 1894, numbered as 4536, 4536A, 4536B, and 4536C (see citations below). Label data of the three lectotype specimens do not specify the year of collection, but a Curtiss collection of F. caroliniana sensu stricto also numbered "2321" was made in 1880 (Georgia, Decatur Co., Oct 1880, Curtiss 2321, GH!).

Fraxinus profunda var. ashei E.J. Palmer, J. Arnold Arbor. 13: 417. 1932. TYPE: USA. Florida. [Suwannee Co.:] near Hildreath, growing in the water, 15 May 1929, W.W. Ashe s.n. (probable holotype: NCU, digital image!). Palmer (1932) did not specifically cite NCU as the herbarium of deposition of the type but he noted that "My attention was first called to this tree by Mr. W.W. Ashe, for whom the variety is named, and on whose notes and collections I have drawn to supplement my own made this season in the region where it grows." There is no specimen at GH of Ashe's collection from near Hildreath and it seems evident that Palmer had a loan of his material from NCU. The NCU sheet is annotated by hand as "type."

Trees 4–10(–15) m tall, usually single-stemmed and erect from the base; twigs terete; winter buds dark brown. Leaves deciduous, pinnately compound, 15–30 cm, leaflets (3–)5(–7), terminal leaflet rarely absent, petioles 3.5–9 cm, bases not raised on pedestals, petiole plus rachis 6–15 cm, petiolules 5–11 mm, blades oblong-elliptic, elliptic, elliptic-lanceolate, or ovate-lanceolate, terminal (5.5–)7–13(–16) cm x (2–)3.5–7 cm, lateral usually slightly smaller, dark green and glossy adaxially, olive abaxially, apices acute to abruptly or gradually acuminate, bases rounded to obtuse or attenuate, lateral veins 7–11 pairs, margins shallowly dentate-serrulate to serrulate on the distal 2/3; petiole base shallowly notched adaxially, leaf scars apically shallowly convex to subtruncate, 3–4(–6) mm wide. Flowers unisexual (species dioecious), appearing before the leaves, wind-pollinated; pistillate calyx ca. 1 mm, persisting at base of samara; petals absent. Samaras 32–47 mm, elliptic-oblanceolate to narrowly obovate, bodies (16–)20–26 mm, flattened, usually channeled along the middle, half or less than half the length of the samara, wings 2, gradually expanded from near the base to middle of the body, (7–)9–10(–12) mm across at widest point, lateral veins 8–12 on each side.

Flowering Mar–Apr. Sloughs, swamps, usually in standing water; 2–20 m; Florida, Georgia. Swamp white ash, pop white ash, water white ash.

Additional collections examined. Florida. Alachua Co.: S of Gainesville, Paynes Prairie State Preserve, hammock NE of Alachua Sink, northern portion of hammock, 10 April 1982, Easterday 858 (FLAS); along Newnans Lake, Gainesville, 13 July 1936, West & Evers s.n. (FLAS). Baker Co.: along Cedar Creek, 5.5 miles N of Glen Saint Mary, 8 Jun 1950, Kurz s.n. (FSU). Bay Co.: bank of Econfina River, E side, 0.8 mile W of Youngstown, 24 Apr 1951, Kurz s.n. (FSU). Clay Co.: Hibernia, Mar 1869, Canby s.n. (NY-3 sheets). Dixie Co.: California Creek, 7.5 mi SSW of Cross City, hammock, partially underwater, limestone undersurface, 8 m tree in water, 13 May 1966, McDaniel 7489 (FSU). Duval Co.: swamps, near Jacksonville — 27 Aug 1894, Curtiss 4536 (NY), 27 Aug 1894, Curtiss 4536A (NY), 2 Jul 1894, Curtiss 4536B (NY), 1894, Curtiss 4536C (NY); 7.5 mi E of Baldwin or 4 mi W of Marietta on U.S. Rte 90, swamp, 7 Jul 1949 Kurz s.n. (FSU); 1-2 mi W of Atlantic Beach, 6 Sep 1949, Kurz s.n. (FSU); 7.8 mi E of Jacksonville city limits on US Rte. A1A, swamp, 7 Jun 1950, Kurz s.n. (GH, VDB); 2.4 miles E of Jacksonville city limits on S side of road at A1A Rte bridge, swamp, 8 Jun 1950, Kurz s.n. (FSU). Flagler Co.: cypress swamp near Andalusia, 18 April 1940, West & Arnold s.n. (FLAS). Jefferson Co.: Jefferson Co.: Wet hammock, 0.5 mi W of Aucilla River, by US Rt. 98, E of Newport, 14 June 1983, Godfrey 80693 (FLAS); slough between

Newport and Aucilla River, growing in 2 feet of standing water, 2 May 1956, Kral & Godfrey 2379 (FLAS, FSU, LL, NY); at junction of the Wascissa River and Aucilla River, in swampy area, small tree (15 feet), [no date], Williams s.n. (FSU). Lafayette Co.: Lafayette Co.: Mallory Swamp Conservation Area, SW of Branford, highly degraded mosaic of bottomland forest and basin swamp, 4 Sept 2004, Abbott 19177 with Heaney (FLAS); on E side of Fla. Rte 51, 9 mi N of U.S. Rte 19, N of Mayo. in water, 5 Sep 1949, Kurz s.n. (FSU, GH). Lake Co.: along W side of the St. Johns River along Fla. Rte 40, 22 Jul 1950, Kurz s.n. (FSU, NY); Tavares, low hammock, 13 June 1940, Murrill s.b. (FLAS); vicinity of Eustis, in water, Lake Norris, small tree 12-15 ft high, 16-25 Aug 1894, Nash 1698 (AA, NY); vicinity of Eustis, cypress swamp at Eldorado, tree 30-50 ft high, 16-25 Aug 1894, Nash 1698 (NY). Levy Co.: Waccasassa Bay State Preserve, well west of Jack's Creek; coastal hydric hammock, with scattered freshwater depressions and scattered areas of mixed hardwoods, 9 June 1997, Abbott 10489 with Judd (FLAS); swamp ca. 6 mi N of Cedar Key, 22 Jul 1960, Godfrey 60102 (SMU). Liberty Co.: floodplain woods along the Ochlockonee River, Rte 20, W of Tallahassee, 2 Jun 1950, Kurz s.n. (NY, VDB); N of Fla. Rte 20, in W floodplain of Ocklockonee River, 2 Jun 1950, Kurz s.n. (FSU); Liberty Co.: Telogia Creek, access road to boat ramp off Co. Rd. 67A, 1.8 air mi ENE of Telogia, common small trees along sloughs and in swamp, ca. 10–25 feet tall, trunks slender, erect, and single, none in fruit, Fraxinus caroliniana common (not collected) and in fruit along sides of creek, 12 Jul 2010, Nesom 2010-F3 (FLAS, GH, NY); W side of Hwy 65 0.6 mi S of jet with Hwy 267 S of Hosford, ca. 50 yards N of bridge over Telogia Creek, edge of swamp, tree 40 feet tall, fruits out of reach and not collected, 12 Jul 2010, Nesom 2010-F4 (FSU, GH, NY, TEX); W side of Hwy 65 0.6 mi S of jet with Hwy 267 S of Hosford, ca. 50 yards N of bridge over Telogia Creek, edge of swamp, small, singe-trunked trees in immediate vicinity of Fraxinus profunda (Nesom F4), not in fruit, 12 Jul 2010, Nesom 2010-F5 (FLAS, GH, NY, TEX). Marion Co.: swamp along Rainbow River, Dunellon, in water, small tree with several trunks from near the base, bases of trunks enlarged, 1 May 1976, Godfrey 74890 (FSU, VDB); riverine forest beneath the Oklawaha River bridge ("Eureka Mountain") along C-316, just E of Eureka, 24 Jul 1985, Hansen & Wunderlin 10456 (TEX); Ocala National Forest, along Mormon Branch, a tributary of Juniper Run, moist forest along creek, 30 July 1994, Judd 8036 (FLAS); W edge of Oklawaha R. swamp, dominant species, with N. sylvatica var. biflora also abundant, 25 June 1975, Martin & Cooper 735 (FLAS); 1/4 mi E of Olawaha River, Eureka, riverbottom swamp, frequent, from upper branches of uprooted tree 45 ft. high, 6 in. diameter, 17 May 1963, Ward & Laessle 3484 (FSU). Nassau Co.: White Oak Plantation in the wedge formed by the jet of the Little St. Mary's River and St. Mary's River, ca. 8-10 mi NW of Yulee, swamp forest 100-200 yards NW of the Pavilion Bldg along the St. Mary's River, tree 6 m tall in standing water, 23 Jul 1997, Wilbur 68108 (BRIT, FLAS). Orange Co.: 5 mi SE of Fort Christmas, in a swamp, 19 Sept 1929, O'Neill s.n. (FLAS). Osceola Co.: deep swamps, near Kissimmee, tall slender tree, 2 Apr 1931, Palmer 38356 (AA, NY). Seminole Co.: Seminole/Lake County, along banks of Wekiva River, dominant, 30 Jun 1990, Bacchus 5492 (FLAS, FSU); 2 mi NW of Sanford on U.S. Rte 17, 22 July 1950, Kurz s.n. (FSU). Putnam Co.: along Oklawaha River, Cedar Landing, 7 July 1935, Arnold s.n. (FLAS). St. Johns Co.: bank of St. Johns River, 27 March 1910, Hood 72069 (FLAS); riverside, Tocoi, 7 June 1940, West & Arnold s.n. (FLAS). Suwannee Co.: 5 mi NW of Fort White off of US 27 in Ichetucknee Springs State Park, ca. 0.2 mi W of Old South entrance, 0.8 mi S of US 27 bridge, floodplain forest and swamp, 6 May 1992, Herring 709 (FLAS). Wakulla Co.: swamp by East River, by first bridge after entering St. Marks National Wildlife Refuge on Lighthouse Rd, single-stemmed tree ca. 9 m tall, 17 Jul 1981, Godfrey 79020 (FLAS, FSU, VDB); river swamps, Aucilla River, 5 mi above mouth, 10 Apr 1934, Griscom 21597 (AA); St. Marks, low woods, 29 Apr 1914, Harbison 1499 (AA); N side of Wakulla River, along U.S. Rte 319, 27 Sep 1949, Kurz s.n. (FSU); E side of Wakulla River, swamp, 14 Jun 1950, Kurz s.n. (FSU); St. Marks NWR, Lighthouse Road (Hwy 59), area of double bridge over East River Pool, ca. 1.8 road mi S of the Refuge Headquarters and Visitor Center, common small trees in standing water, few in fruit, trunks erect, single, 13 Jul 2010, Nesom 2010-F6 (FLAS, GH, NY); St. Marks NWR, Lighthouse Road (Hwy 59), area of double bridge over East River Pool, ca. 1.8 road mi S of the Refuge Headquarters and Visitor

Center, single tree at edge of swamp, above water level, trunk single, erect, ca. 40 feet tall, profusely fruiting, 13 Jul 2010, 2010-Nesom F7 (FSU, GH); W side of Wakulla River, swamp along N side of Hwy 319/95, ca. 3 air mi NW of town of St. Marks, common trees, trunks single, erect, 10-40 feet tall, few in fruit and fruits high and out of reach, 13 Jul 2010, Nesom 2010-F8 (FLAS, FSU, GH, NCU, NY, TEX); near Rd 59 ca 6 mi N of the St. Marks Lighthouse, cypress-hardwood swamp, abundant, tree up to 20 feet tall, 20 Jun 1950 Redfearn 2510 (FSU, GH). Walton Co.: Choctawhatchee River delta, 12 April 1975, Suttkus 75-6-12 (FLAS). Washington Co.: E edge of Caryville, 20 Aug 1950, Kurz T-3 (FSU). Georgia. Charlton Co.: along St. Mary's River, Trader's Hill section, 15 Apr 1940, Kelley 50 (AA); St. Mary's River swamp, below Trader's Hill, 12-15 Jun 1895, Small s.n. (AA, NY); St. Mary's River swamp, below Trader's Hill, 24-26 Jul 1895, Small s.n. (AA, NY). Decatur Co.: at easternmost bridge at head of Florida Sterile Hospital Pond, near Jink's Siding, NE of Chattachoochee, in creek swamp, 19 Aug 1975, Gholson 4562 (FLAS). Dougherty Co.: along the Flint River at Albany, 24-28 May 1895, Small s.n. (AA, NY). Citations of collections from FLAS are provided by Walter Judd, who identified the specimens.

In the Trader's Hill area of southeastern Georgia, whence the type of Fraxinus pauciflora, collections also have been made of F. caroliniana. J.K. Small collected both species there in June of 1895. USA. Georgia. Charlton Co.: St. Mary's bottomland, Thompson's Landing, 21 Jul 1958, Cypert 113 (GA); branch of St. Mary's River, Trader's Hill, small tree, 3 Apr 1918, Harbison 4 (AA); St. Mary's River, Cedar Landing, river swamp, 31 May 1930, Harper 231 (GH); in the St. Mary's River swamp, below Trader's Hill, 12-15 Jun 1985, Small s.n. (AA).

The abaxial leaf surface of *Fraximus pauciflora* has a distinctive morphology otherwise known only in the *F. americana* group (*F. americana*, *F. biltmoreana*, *F. smallii*, and *F. albicans*). This is easily observed with a dissecting microscope (40X) and once the nature of the character is understood, a 10–20X hand lens may be sufficient to make the observation.

Lingelsheim (1908) was fully aware of the distinctive abaxial leaf morphology of *Fraximus* americana and upon studying specimens of *F. pauciflora* from Florida recognized the similarity in this feature of these water ash trees to white ash. His explicit speculation that they were hybrid in origin between *F. americana* and *F. caroliniana* was reflected in his choice of epithet.

Collections at NY of Fraxinus pauciflora studied by Gertrude Miller were annotated by her (on 25 May 1951) as "Fraxinus americana complex" or in a few cases as "Fraxinus americana L.—caroliniana Mill." Earlier, at GH in 1950, she had annotated some collections of F. pauciflora as "F. floridana Sarg.?" She was aware of the epidermal distinction and in her monograph (Miller 1955, p. 25) she observed that these trees, which she knew at the time only from Lake County, Florida, "seem to be the result of a rare or chance hybrid between a member of the red ash complex and one of the white ash complex. ... This hybrid has persisted at or near the point where the original hybrid appeared, but has not been able to extend its range, or only very slightly. Until more evidence becomes available, and largely for convenience, in this study the hybrid is arbitrarily called F. caroliniana Mill. – americana L.?"

Sargent (1902, p. 39, plate 717) also separated Fraxinus caroliniana and F. pauciflora (using the name F. floridana for the latter), observing that "A small Ash-tree which grows in ponds and deep river-swamps in eastern and western Florida and in southern Georgia and which has usually been considered a form of the Water Ash, Fraxinus Caroliniana, varies constantly from that species in the form of the fruit. It is desirable that a plate of this second species of Water Ash should appear in a Silva of North America, and although the foliage and winter-buds do not afford characters by which the two trees can be readily distinguished in the herbarium, it is convenient to treat them as species rather than as varieties." Sargent's note that collections of F. floridana were made "near Jacksonville,"

Eustis, and Apalachicola, Florida, and in Charlton County, southern Georgia" leave little doubt that it is the same species identified here as F. pauciflora.

In limited field study in northern Florida (two days in Franklin, Liberty, Leon, and Wakulla counties), I saw *Fraxinus caroliniana* only along the immediate sides of creeks and rivers. *Fraxinus pauciflora* apparently is much more common in that area, occurring within and along the edges of swamps. Only a small percentage (ca. 10–20%) of the *F. pauciflora* trees were in fruit. In other areas, however, label data indicate that *F. caroliniana* sensu stricto has a broader ecological range.

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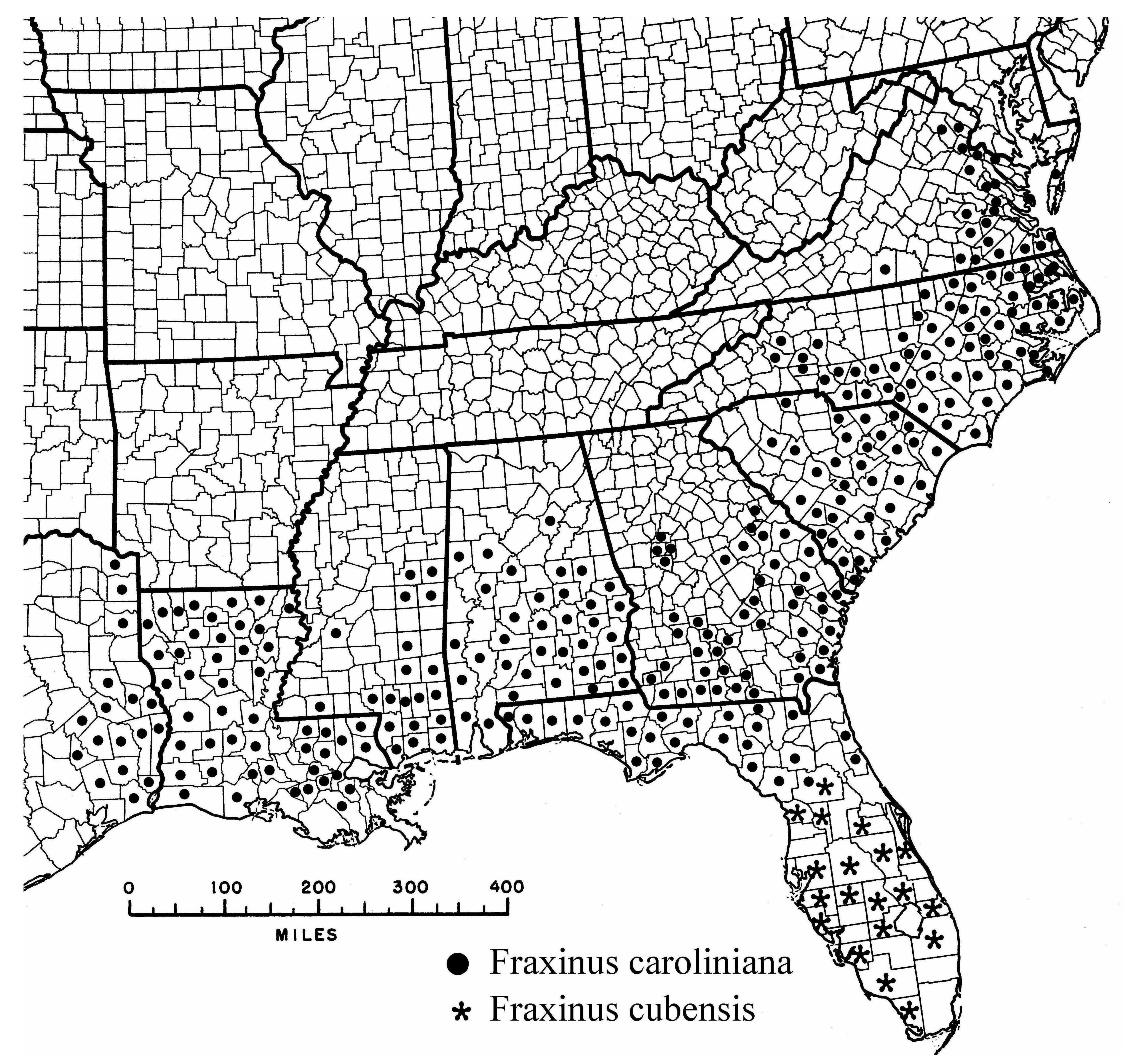


Figure 1. Distribution of Fraxinus caroliniana and F. cubensis. Fraxinus cubensis also occurs in western portions of Cuba (see text).

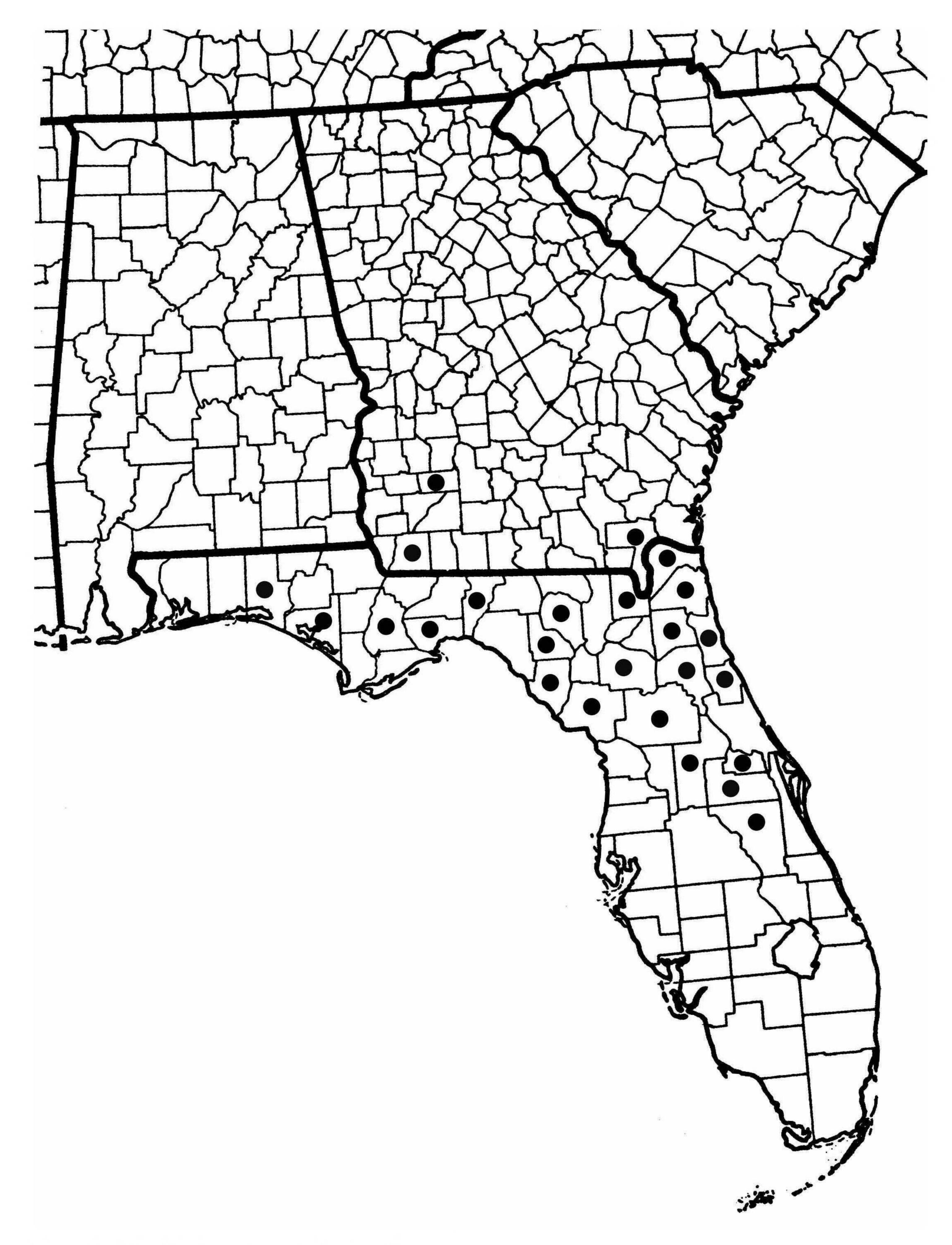


Figure 2. Distribution of Fraxinus pauciflora.



Figure 3. Representative samaras of Fraxinus pauciflora.



Figure 4. Representative samaras of Fraxinus cubensis.



Figure 5. Representative samaras of Fraxinus caroliniana.